EVIDENCE FOR DIRECTIONAL SELECTION ON MALE ABDOMEN SIZE IN *MECOLAESTHUS LONGISSIMUS* SIMON (ARANEAE, PHOLCIDAE)

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ABSTRACT. Abdomens of male *Mecolaesthus longissimus* Simon 1893 are on average more than twice as long as in females, their length is highly variable, and they show extremely steep allometric values when scaled on body size (OLS, b = 2.64). Males cohabit with females, and they likely fight to defend this position as other pholcid spiders do. Male legs, which are usually used in pholcid male-male fights, do not show the usual high allometric values but a very low value (OLS, b = 0.37). Collectively, this lends support to the idea that *M. longissimus* males do not use their legs in fights and that male abdomens have assumed a role in male-male fights. However, behavioral data are missing and sexual selection by female choice or inter-male display might be involved. A large sample of data from taxonomic revisions is used to document that across pholcids, males consistently have longer tibiae 1 (and probably legs in general) than females. Several possible reasons have been suggested to account for longer male than female legs in various spider groups, but the pattern in pholcids remains to be explained.

Keywords: Sexual size dimorphism, sexual selection, allometry, Pholcidae

Extreme sexual size dimorphism in spiders has attracted considerable attention for a long time and its evolutionary origin has fueled a lively and ongoing debate (Vollrath & Parker 1992; Coddington et al. 1997; Head 1995; Prenter et al. 1997, 1998, 1999; Hormiga et al. 2000; Schneider et al. 2000; Moya-Laraño et al. 2002; Walker & Rypstra 2003). The more common case of slight size dimorphism and the rather exceptional case of males being larger than females have remained comparatively out of the main focus of size dimorphism studies in spiders (but see Prenter et al. 1995, 2003; Toft 1989; Schütz & Taborsky 2003). Different selective forces, both natural and sexual, probably interact in many species, but fecundity selection may be the single major factor responsible for females usually being larger than males (Beck & Connor 1992; Elgar 1992; Head 1995; Prenter et al. 1999). However, simple size measures derived from the taxonomic literature may result in an overly simplistic view of dimorphism. Depending on the structure measured, either males or females may appear to be the 'larger' sex, and some or most dimorphism may be in shape rather than in size (Prenter et al. 1995).

Few cases of males being larger than females are known in spiders (Prenter et al. 1999; Lång 2001) even though large male size advantage has been documented in numerous species (Vollrath 1980; Elgar & Nash 1988; Nielsen & Toft 1990; Dodson & Beck 1993; Kotiaho et al. 1997, 1999; Elgar 1998; Elgar & Fahey 1996; Taylor et al. 2001; Prenter et al. 2003; Schaefer & Uhl 2003). In most cases in which males are larger than females, male-male fights are intense, and winners of contests sire a significant proportion of their mate's offspring (Rovner 1968; Watson 1990; Elgar 1998). Selection is particularly strong on the fighting structures per se (e.g., chelicerae in certain linyphiid and salticid spiders: Rovner 1968; Toft 1989; Pollard 1994; Funke & Huber In press) and such intense directional selection usually results in high allometric values (i.e. > 1.0; Petrie 1992; Green 1992; Baker & Wilkinson 2001; Tatsuta et al. 2001; Funke & Huber In press; see also Eberhard et al. 1998; Eberhard 2002a, b). Natural selection may also result in males being the larger sex, as in the exceptional case of the water spider, *Argyroneta aquatica* (Clerck 1757). In this species, males are on average nearly 30% larger than females, as a result of the unusual habitat (Schütz & Taborsky 2003).

The presence and degree of sexual size dimorphism within and among species can be
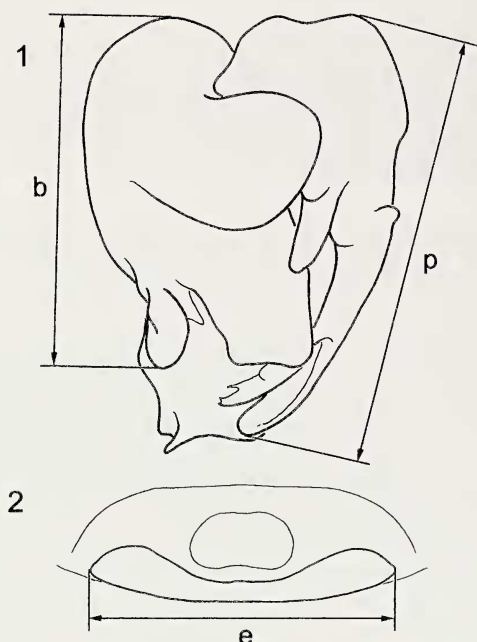
Figures 1, 2.—*Mecolaesthus longissimus*, genitalic characters measured. 1. Bulb length (b) and procursus length (p), dorsal view; 2. Epigynum width (e), ventral view.

used to generate behavioral hypotheses that can then be tested. In this study, I have two main objectives: (1) to document and quantify the apparently unique dimorphism observed in the pholcid *Mecolaesthus longissimus*, and (2) to use data from the literature to quantify leg length dimorphism across pholcid species.

The main object of this study, *Mecolaesthus longissimus* Simon 1893, is endemic to the Cordillera de la Costa in northern Venezuela (Huber 2000). Nothing is known about its biology except for some very basic habitat data (Simon 1893; Huber 2000).

METHODS

Males and females of *Mecolaesthus longissimus* were collected in a forest above Colonia Tovar (10°25′N, 67°18′W), 2100 m a.s.l., Aragua, Venezuela, on 26 November 2002, by the author. The present analysis is based on a sample of 30 males and 14 females preserved in 80% ethanol. They are presently deposited at the Zoological Research Institute and Museum Alexander Koenig, Bonn, but will later be partly transferred to the Museo de La Salle, Caracas. Drawings were made with a camera lucida on a Leitz Dialux 20 compound micro-

scope. Photos were made with a Nikon Coolpix 995 digital camera (1600 × 1200 pixels) mounted on a Nikon SMZ1500 dissecting microscope.

Measurements were made with an ocular grid on a Nikon SMZ1500 dissecting microscope. Tibia length was measured dorsally; carapace length was measured medially from anterior median eyes to posterior border; abdomen length was measured ventrally from frontal end to base of frontal spinnerets; anterior and posterior parts were divided by the epigastric furrow, resulting in two measures; for genitalic measures see Figs. 1 and 2. Genitalia were included in the analysis to support the assumption that all specimens included are indeed the same species. Statistical analysis was done with SPSS 11.0. Ordinary least squares (OLS) and reduced major axis (RMA) regressions of log-transformed characters were calculated for all traits on carapace length as an indicator of body size (for critique and justification of method see Green 1999 and Eberhard et al. 1999). Carapace length was used rather than carapace width (the usual indicator of body size in spiders) because lateral carapace borders appeared too soft and indistinct.

For comparison of male and female tibia 1 lengths in pholcid spiders, data were taken from recent revisions (Huber 1997a, b, c; 1998a, b, 2000, 2001, 2003a, b, c; Huber & Pérez 1998, 2001; Huber et al. In press; B.A. Huber unpubl. data). In order to be included in the analysis, the species (re)description had to give a mean value of at least five measured tibiae 1 in each sex. All together, 2673 tibia 1 measures of 100 species (20 of them unpublished) were included, representing 28 genera and all four pholcid subfamily-level taxa. The complete data matrix is available from the author.

RESULTS

Morphometric analysis of *Mecolaesthus longissimus*.—Three details are noteworthy in the morphometric analysis (Table 1). First, male abdomens are on average more than twice as long as female abdomens (see also Figs. 4, 8, 9). Second, male abdomens are extremely variable (see also Figs. 5–7 & 9). Third, it is the anterior part of the male abdomen that accounts for most of the variation in male abdomen length. In females, to the
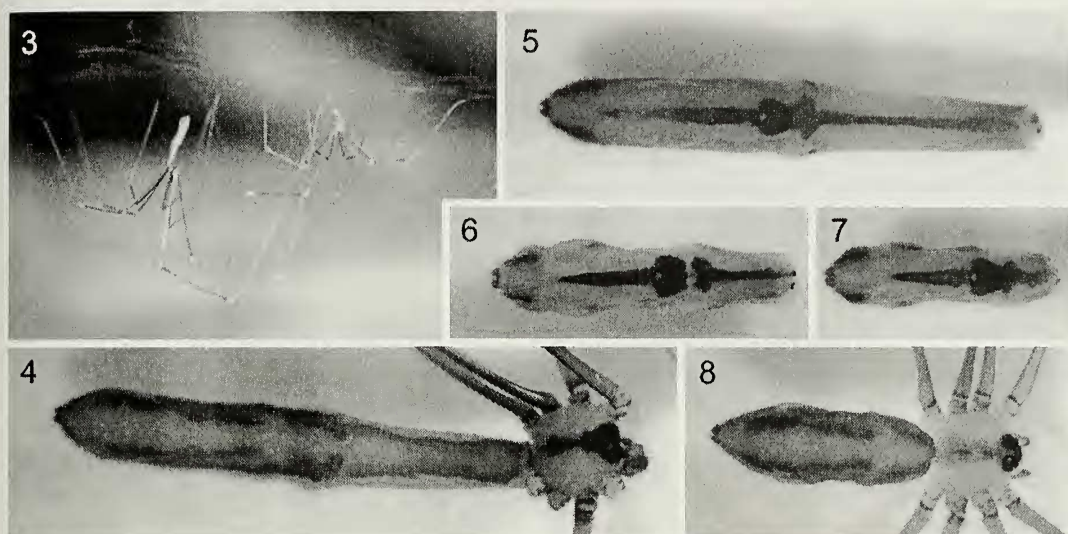
Figures 3–8.—*Mecolaesthus longissimus*. 3. Male (left) and female in the web (photo courtesy B. Striffler); 4. Large male, dorsal view; 5–7. Large, medium, and small male abdomens, ventral views; 8. Medium size female. Figs. 4–8 are to the same scale.

contrary, it is the posterior part of the abdomen that is much more variable than the anterior part.

No appreciable shape variation was seen in the structures usually used in species discrimination in pholcids (male procursus, bulbal sclerites, cheliceral armature). The regression coefficients of the three genitalic structures measured were low as is usual for genitalia (Eberhard et al. 1998). Surprisingly low regression values were also found for male (but not female) legs.

Comparative analysis of pholcid tibiae 1.—There is a consistent trend for males to have longer tibiae 1 than females when 100 species were compared (Fig. 10). The mean ratio of male/ female tibia 1 is 1.28, the median 1.27 (Fig. 11). Strictly speaking, species are linked by phylogeny and not independent data points (Harvey & Pagel 1991). However, my aim here is to document a universal trend within the family and not to claim that there are independent events that might justify some adaptive explanation. Regardless of the details of the phylogeny of pholcids, parsimony clearly suggests that ancestral pholcids had longer male than female legs.

DISCUSSION

The extremely high allometric value of male abdomen length in *M. longissimus* indicates that directional selection is operating on this body part. Structures used as weapons in male-male fights or as visual display characters in the context of sexual selection tend to show high allometric values (Petrie 1992; Green 1992; Baker & Wilkinson 2001; Tatsuta et al. 2001; Funke & Huber In press; see also Eberhard et al. 1998; Eberhard 2002a, b). The exact nature of this selection cannot be derived from allometric values alone but only by behavioral observations and experiments. However, circumstantial evidence suggests that males might use their abdomens in a most unusual and unexpected way: as display or even fighting devices.

First, male-female postinsemination non-contact guarding (*sensu* Alcock 1994) is rare in spiders (Elgar 1998) but common in pholcids (Eberhard & Briceño 1985; Kaster & Jakob 1997; pers. obs.). For example, during a monthly survey of a population of *Modisimus guatuso* Huber 1998 in Costa Rica from November 1995–September 1997, I counted 398 pairs involving adult males and adult females, not a single pair involving a juvenile female, and 65% of 596 males seen were cohabiting (unpub. data). During several collecting expeditions I have become used to the expectation that seeing one adult pholcid often means that another one of the opposite sex is nearby. Most webs at the collection site of the present species contained a male and a mature female.

Table 1.—*Mecolaesthus longissimus*, male and female characters measured (in mm), with sample sizes (*n*), ranges, means, standard deviations (SD), coefficients of variation, corrected for sample size (CV*), significance values of Kolmogorov-Smirnov tests for normal distribution (KS), estimates on measurement error ($\pm$ 1/2 unit on the measuring grid), and slopes (b) of regressions on carapace length as an indicator of body size, using ordinary least squares (OLS) and reduced major axis (RMA) regression. Slopes significantly different from 0 are indicated by *($P < 0.05$), **($P < 0.01$), and ***($P < 0.001$). RMA regressions were not calculated when OLS values were non-significant.

Characters	n	Range	Mean	SD	CV*	KS	Measurement error ($\pm$ mm)	b (OLS)	b (RMA)
Males									
tibia 1 length	30	10.53–12.80	11.59	0.54	4.7	0.57	0.07	0.37***	0.57
tibia 3 length	30	5.15–6.40	5.78	0.31	5.3	0.69	0.05	0.49***	0.66
abdomen total length	30	2.90–6.50	4.85	1.21	25.1	0.33	0.07	2.64***	3.14
abdomen frontal part	30	1.15–3.80	2.42	0.90	37.5	0.32	0.03	3.72***	4.67
abdomen post. part	30	1.75–2.95	2.44	0.36	15.1	0.75	0.07	1.60***	1.93
carapace length	30	0.90–1.22	1.09	0.088	8.2	0.84	0.01	—	—
bulb length	30	0.35–0.38	0.36	0.009	2.4	0.10	0.005	0.21***	0.29
procursus length	30	0.39–0.43	0.41	0.012	2.9	0.16	0.005	0.23***	0.35
Females									
tibia 1 length	10	6.55–8.10	7.38	0.46	6.4	0.71	0.07	1.91**	2.37
tibia 3 length	14	3.05–3.78	3.51	0.21	6.1	0.71	0.03	1.39**	2.11
abdomen total length	14	2.00–2.70	2.34	0.18	7.9	1.00	0.02	1.07 n.s.	—
abdomen frontal part	14	0.82–0.92	0.88	0.031	3.6	0.52	0.02	0.45 n.s.	—
abdomen post. part	14	1.17–1.80	1.46	0.17	11.6	1.00	0.02	1.43 n.s.	—
carapace length	14	0.80–0.90	0.85	0.026	3.1	0.78	0.01	—	—
epigynum width	14	0.34–0.39	0.36	0.013	3.6	0.90	0.005	0.37 n.s.	—

(The reason that many more males were collected is simply that I always collected the males first in order to maximize the male sample, and females often dropped out of the web before I could capture them.) *Pholcus phalangioides* (Fuesslin 1775), the pholcid species studied in most detail, is apparently unusual in this regard as there is no evidence for mate guarding (Uhl 1998).

Fights have been observed in pholcids (Eberhard 1992; Eberhard & Briceño 1985), and it is probable that males gain something by cohabiting with or guarding females and that they will fight to defend whatever resource there is. The exact benefit males derive from staying with females is unknown. They might protect their sperm investment from competition with rival male ejaculates, because in pholcids the second males may fertilize a large proportion of eggs (Eberhard et al. 1993; Kaster & Jakob 1997; Yoward 1998; Schäfer & Uhl 2002). They might improve female foraging efficiency, but chivalrous behavior in pholcids might rather be a means to induce the female not to leave and thus make her defensible (Eberhard & Briceño 1983). They might aid the female to repel other motivated males (Parker 1970). Finally, they might provide postinsemination signals to increase their chances of fathering their mate's
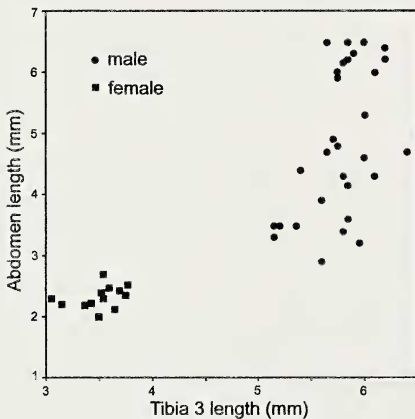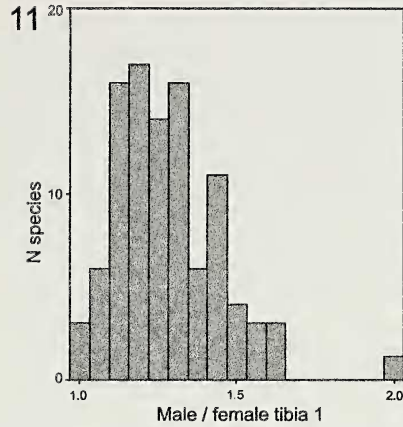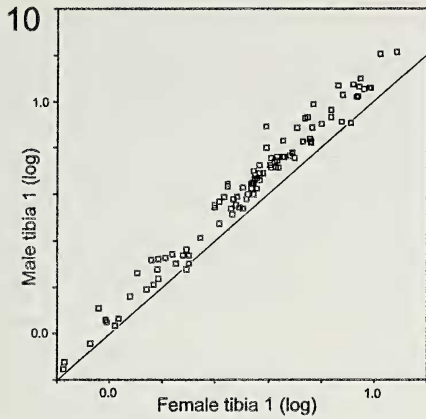

Figure 9.—*Mecolaesthus longissimus*, scatter of male and female abdomen lengths on tibia 3 lengths.

Figures 10, 11.—Tibia 1 length dimorphism in Pholcidae. 10. Scatter of log-transformed male tibia 1 lengths on female tibia 1 lengths for 100 pholcid species. The line indicates monomorphism; 11. Histogram showing the ratio of male/female tibia 1 lengths in 100 pholcid species.

offspring (Eberhard 1985; Alcock 1994). Whatever the details, male *M. longissimus* probably fight intruders, or try to expel residents.

Second, exaggerated morphologies and high variability of sexually dimorphic characters often seem to result from sexual selection (Pomiankowski & Møller 1995; Baker & Wilkinson 2001). For example, extreme male size variation in the salticid *Zygoballus rufipes* Peckham & Peckham 1885 was attributed to alternative male mating strategies (Faber 1994). Comparative evidence strongly suggests that female *M. longissimus* have retained the plesiomorphic abdomen size, and that males vary from 'normal' to extreme. All other known species of *Mecolaesthus* have 'normal' abdomens, not appreciably different from the abdomens of females and of other closely related genera (Huber 2000). Thus, male *M. longissimus* abdomens are exaggerated sexual modifications.

Third, there is no evidence pointing to ecological determinants of male abdomen size. The webs in which the specimens were collected appear identical to those of many New World pholcids, i.e. a distinct, loosely meshed and more or less domed sheet (Eberhard & Briceño 1985). Further observations on ecology are not available.

Thus, sexual selection on male abdomen size appears as the most plausible explanation for the dimorphism in this species. Female choice might be involved, and a large abdomen may be a costly and thus honest indicator of male quality (cf. Uetz et al. 2002). Alternatively, cryptic female choice might select for exaggerated male testes or accessory genital glands (cf. Eberhard 1996). However, numerous studies indicate that male-male fights are the most important force selecting for large male size (Christenson & Goist 1979; Watson 1990, 1991; review in Andersson 1994). Therefore, I hypothesize that male *M. longissimus* use their abdomens either to fight or to assess each other before fights. A large brown spot ventrally on the abdomen (Figs. 5–7) might be significant in this respect: the spot marks the posterior border of the anterior part of the abdomen, i.e. that part that is most extremely size dimorphic, has the highest regression coefficient, and is therefore the most reliable predictor of male size (cf. Taylor et al. 2000). Male *M. longissimus* carry their abdomen more or less vertically (Fig. 3; see also fig. 439 in Simon 1893), making the spot potentially visible to conspecifics in the same web. Whether pholcids have the appropriate visual capabilities is unknown.

A surprising but revealing result is the low regression value of male (but not female) tibia 1 (b[OLS] = 0.37) in *M. longissimus*. It is consistently higher in other pholcids studied: 0.88 in *Metagonia mariguitarensis* (González-Sponga 1998) (Huber 2004), 1.00 in *Buitinga safura* Huber 2003 (Huber & Hopf 2004), 1.22 in *Physocyclus globosus* (Taczanowski 1874) (Eberhard et al. 1998). This would seem to indicate stabilizing selection in *M. longissimus*, in contrast to other pholcids. I hypoth-

esize that the unusual regression value of male leg length and the unusual exaggerated abdomen are directly correlated and that *M. longissimus* males have changed from leg fights (the usual strategy in pholcids: Eberhard 1992; Eberhard & Briceño 1985) to abdomen fights, thus relaxing selection on leg length. However, this still requires an explanation for longer legs in *M. longissimus* males than in females. One potential explanation is phylogenetic inertia, as nearly all pholcids have longer male than female legs (see below).

The tibia 1 measures across the entire family clearly show that male pholcids have consistently longer tibiae than females. Unfortunately, there are no comparable data on other size measures, as for example total body size. However, the reason for this missing data is that male and female pholcids usually are monomorphic regarding total size (Elgar 1992; pers. obs.). Collectively, this lends further support to the idea that single size measures may not reliably reflect sexual size dimorphism in spiders (Prenter et al. 1995). The reasons for leg length dimorphism in pholcids are unknown. Longer legs may help cursorial males in their search for females (Montgomery 1910), they may provide males with a wide sensory radius and keep them relatively safe from female aggression (Elgar et al. 1990), or they may play a role in male-male fights (Eberhard 1992; Dodson & Beck 1993; Eberhard & Briceño 1985; Prenter et al. 1995; Bridge et al. 2000). Whatever the details, the consistent and fairly uniform pattern argues for a widely responsible cause or set of causes rather than for varying explanations in different taxa.

ACKNOWLEDGMENTS

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